Agarics and Boletes of Neotropical Oakwoods 1

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Introduction

The agarics and boletes in Neotropical forests exhibit several different patterns of origin and distribution. The patterns and diversity are directly related to the types of habitats in which these fungi occur and have been influenced by geological history, native and introduced phanerogamic vegetation, climate and, ultimately, human impact. Specifically, the aforementioned factors affect the distribution of those agarics and boletes that occur naturally in the montane oak forests of Costa Rica and Colombia. Much of the descriptive literature documenting the diversity of Neotropical, montane oak forest agarics and boletes has been cited previously (Halling and Franco-M., 1996; Halling and Mueller, 1999).

Others have speculated previously on the biogeographic connections of a few agaric genera and species (e.g. Guzmán, 1974; Moser and Horak, 1975; Halling and Ovrebo, 1987; Guzmán *et al.*, 1989; Mueller and Strack, 1992; Mueller and Halling, 1995; Halling, 1997a). Based on concentrated fieldwork in Central and South America over the last decade, with particular emphasis on ectomycorrhizal fungi, a mass of data has been compiled, the interpretation of which suggests clear biogeographic tendencies or connections.

Trappe (1977) postulated that the present disjunct distribution of many truffle-like fungi (Fig. 1.1) in Europe and North America, which are dependent on animals for dispersal, is best explained by their widespread occurrence throughout Laurasia prior to the tectonic events that broke up the animals' overland migration routes some 50 million years ago. While it is commonly

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accepted that above ground forms, like mushrooms, were ancestral to those that are truffle-like (e.g. Thiers, 1984; Bruns *et al.*, 1989; Mueller and Pine, 1994), those mushrooms that had the potential to form ectomycorrhizas would have had to have originated at some point before the 50 million year mark. Based on molecular clock dating of DNA sequences, Berbee and Taylor (1993) suggested that divergence of the homobasidiomycetes occurred in the Triassic, ~220 million years ago ± 50 million years. According to Newman and Reddell (1987), 95% of the *Pinaceae* form ectomycorrhizas. If we assume that the *Pinaceae* are monophyletic and plesiomorphic ectotrophs then *Compsostrobus*, a late Triassic fossil that is thought to be an ovulate cone of *Pinaceae* (Delevoryas and Hope, 1987), suggests that ectomycorrhizal homobasidiomycetes could have arisen by ~200 million years ago (Hibbett *et al.*, 1997). Ectomycorrhizal fungi probably diversified later in the Jurassic (208–146 million years ago), when ectomycorrhizal gymnosperms had become globally established before the breakup of Pangaea. The subsequent diversification of angiosperms was probably a catalyst for a boost in the diversity of ectomycorrhizal fungi soon after these plants appeared in the Cretaceous (146–165 million years ago) (Raven and Axelrod, 1974; Talent, 1984; Truswell *et al.*, 1987).

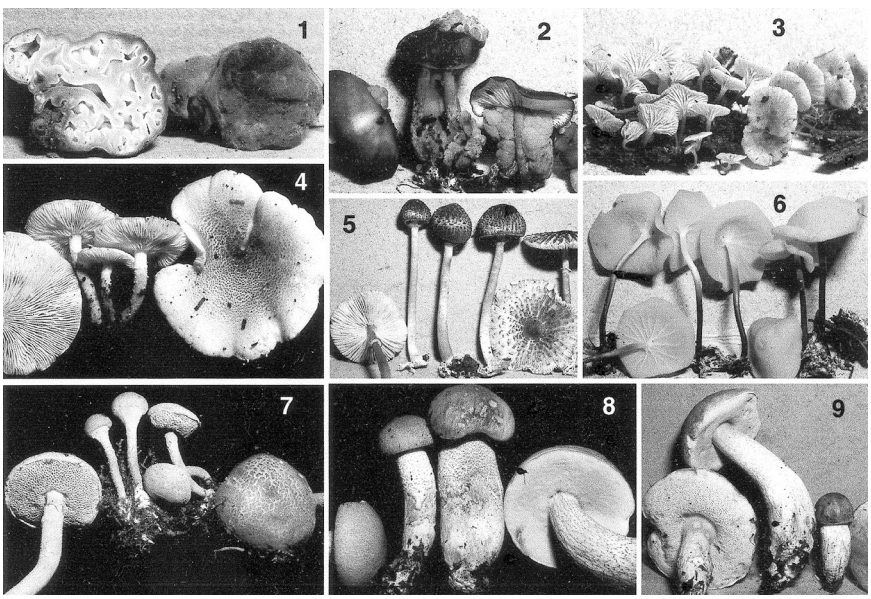

Fig. 1.1. *Hydnotrya tulasnei* (× 0.58). **Fig. 1.2.** *Gymnopus nubicola* with *Syzygospora* parasite (× 0.39). **Fig. 1.3.** *Xeromphalina kauffmanii* (× 0.77). **Fig. 1.4.** *Ripartitella brasilensis* (× 0.39). **Fig. 1.5.** *Rugosospora pseudorubiginosa* (× 0.39). **Fig. 1.6.** *Hymenogloea papyracea* (× 0.19). **Fig. 1.7.** *Pulveroboletus ravenellii* (× 0.58). **Fig. 1.8.** *Tylopilus chromapes* (× 0.19). **Fig. 1.9.** *Tylopilus cartagoensis* (× 0.19).

Stratigraphic evidence in Mesoamerica suggests that the closure of the Panamanian Isthmus occurred from about 3.5–2.4 million years ago in the mid-Pliocene (Marshall and Sempere, 1993; Graham, 1995) allowing for biotic interchange in both directions across latitudes between North and South America. The closure of this portal becomes relevant in the discussion of the recent age of oak forests in South America.

Since the mid to late 1950s, after centuries of deforestation, many areas of the montane Neotropics and elsewhere in the temperate zones were reforested with plantations of exotic trees, namely *Pinus* and *Eucalyptus* spp. The commercial nursery stock of these trees was apparently inoculated with only a few mutualistic mycorrhizal fungi, *Amanita muscaria* (L. : Fr.) Hook. and *Suillus luteus* (L. : Fr.) Gray in particular for pines, and *Laccaria fraterna* (Cooke & Massee: Sacc.) Pegler and *Hydnangium carneum* Wallr. apud Klotzsch for *Eucalyptus*. For example, the Cotopaxi volcano in Ecuador harbours an exotic Monterey pine forest which produces, from personal observation, fruitings of *Suillus luteus* all the year round, to the exclusion of other macrofungi. It is interesting to note that in its native range in California, Monterey pine does not have *S. luteus* as a mycorrhizal symbiont as observed by the authors and H.D. Thiers (California, 1984, personal communication).

In native montane habitats such as the páramo regions above the timberline exemplified by a zone around the Chimborazo volcano in Ecuador, where frost may occur any day of the year, saprobic agarics occur that have north temperate affinities, for example: *Leptonia serrulata* (Fr.) Kummer, and a relative of *Gymnopus dryophilus* (Bull. : Fr.) Murr., named *Gymnopus nubicola* Halling. In its migration from the north, the latter was accompanied by its obligate north temperate parasite, *Syzygospora* (Fig. 1.2). In this zone above the timberline, there are no ectomycorrhizal agarics.

Other non-Andean, montane habitats include the harsh environment of the sandstone table mountains (tepuis) of the Guyana Highlands in north-eastern South America (like Mt Roraima, which inspired A. Conan Doyle's *The Lost World* (1912)). The bizarre vascular plant flora was first explored by the Schomburgk brothers and Everard Im Thurn, and has been extensively documented by Basset Maguire and collaborators since the mid-1950s (Maguire *et al.*, 1953). These regions have been little explored by mycologists. The summits of these tropical plateaux are often rocky, or dominated by open, extremely wet, savanna type vegetation with a low pH. However, in areas inhabited by gallery forest where leaf litter or dead wood accumulates, *Xeromphalina nubium* Redhead & Halling (1987) occurs whose sister species appears to be *Xeromphalina kauffmanii* A.H. Sm. (Fig. 1.3), a North American agaric that grows on oak logs and has a southern distribution limit in the oak forests of montane Panama.

On the other hand, agarics of lowland rainforests exhibit widespread to restricted patterns of distribution but appear not to have species overlap with the temperate zones. Examples here include the pantropical *Ripartitella brasiliensis* (Speg.) Singer (Fig. 1.4), and the amphiatlantic genus *Rugosospora* (*R.*

pseudorubiginosa (Cifuentes & Guzmán) Guzmán & Bandala) (Fig. 1.5), whose Neotropical existence was first noted by Cifuentes and Guzmán (1981). A widespread Neotropical example is provided by *Trogia cantharelloides* (Mont.) Pat. Apparent endemics of lowland to submontane Central America and South America comprise the marasmioid *Hymenogloea papyracea* (Berk & M.A. Curtis) Singer (Fig. 1.6) and the recently described *Marasmiellus volvatus* Singer. However, the known distribution of the latter may just be a reflection of where it has been encountered in under-collected habitats by fortunate, knowledgeable agaricologists.

In montane ectomycorrhizal habitats, Neotropical oak forests are narrowly restricted to the main cordilleras of Mexico, southwards through the Andes to southern Colombia. Dating of pollen in core samples in the vicinity of Bogotá, places their appearance at ± 340,000 years ago (Hooghiemstra and Cleef, 1995). These fossil data indicate that oak is a recent immigrant to central and northern South America. Oaks are abundant and speciose in North America and Mexico, but in Costa Rica there are just ± 12 species (Burger, 1977), whereas in Colombia there is only one. In Costa Rica, according to Kappelle *et al.* (1992), 80% of the canopy and 95% of the basal area of montane forests in the Cordillera Talamanca consist of oaks, whereas 75% of all other plant genera in the understorey and subcanopy are of tropical origin. The agarics and boletes found in these forests show definite affinities with North Temperate taxa and they undoubtedly migrated southward from Mexico with those forest communities.

Documentation and personal observations of ectomycorrhizal associations and distributions during the last two decades have revealed some distinctive patterns: (i) relictual disjunct distributions; (ii) generic and specific distributions along a cline; (iii) local endemism; (iv) high generic similarity; (v) low species similarity; and (vi) high levels of macromycete diversity. These patterns are discussed below in more detail.

Relictual Disjunct Distributions

Based on its current distribution, *Pulveroboletus ravenellii* (Berk. & M.A. Curtis) Murr. (Fig. 1.7), in its many morphs, exhibits a relictual disjunct distribution (personal observation). It is likely to have an ancient genome with minor phenotypic change, and is a generalist in its mycorrhizal associations. It partners with *Pinaceae* and various dicotyledonous genera in eastern and western North America. In its southern distribution in the Americas, *P. ravenellii* associates solely with *Quercus*. It is also reported from *Fagaceae* forests in south-eastern Asia (Corner, 1972), *Myrtaceae* and *Casuarinaceae* in Queensland, Australia (personal observation), but it is notably absent in Europe.

Tylopilus subgenus *Roseoscabra* (typified by *Tylopilus chromapes* (Frost) A.H. Sm. & Thiers fide Wolfe and Bougher, 1993) (Fig. 1.8) presents a slightly different scenario. Wolfe and Bougher (1993) added eight species to the original *T.*

chromapes, including *Tylopilus cartagoensis* C.B. Wolfe & Bougher (Fig. 1.9) from Costa Rica and *Tylopilus queenslandianus* C.B. Wolfe & Bougher from Australia among others. These same authors speculated that there was a Laurasian origin of the ancient genotype, and subsequent migration to and speciation in Australia during Pleistocene glaciations via land bridges. Today known associates are *Pinaceae*, *Fagaceae*, *Betulaceae*, *Salicaceae*, *Myrtaceae*, *Mimosaceae*, and *Casuarinaceae* (known distribution areas of the subgenus are: eastern USA, Costa Rica, Japan to China to north-east Australia but not in Europe). Again, subgenus *Roseoscabra* probably represents an ancient genome, with a generalist mycorrhizal proclivity, but with some phenotypic change or genetic drift/allopatric speciation.

Rozites is an obligately ectomycorrhizal agaric with three known species in the Northern Hemisphere (*Rozites caperata* (Pers. : Fr.) P. Karst. and the recently described *Rozites colombiana* Halling & Ovrebo, and the locally restricted *Rozites emodensis* (Berk.) Moser from the Himalayas). Recently, Bougher *et al.* (1994) indicated that *Rozites* has essentially a Gondwanan distribution and appears to have co-evolved with a Cretaceous fagalean complex with more genetic diversity going south (18 species known today), where it co-evolved with *Nothofagus* (Australia, New Zealand, Chile, Argentina, New Caledonia, Papua New Guinea) and/or with *Myrtaceae* (in Australia). Lesser diversity clearly evolved in the Northern Hemisphere (only three species) after continental breakup. We know that *Nothofagus* was distributed across southern Australia when it rafted away from Antarctica, but it gradually became extinct in part of its range with increasing aridity across in the region known as the Nullarbor Plain. Fossils of *Nothofagus* on that continent and its existence in South America and elsewhere have been the subject of much biogeographical debate (references cited in Bougher *et al.*, 1994). When *Nothofagus* became extinct in south-western Australia in the Eocene/Pliocene, Bougher *et al.* (1994) speculated that the relictual *Rozites symeae* Bougher, Fuhrer, & Horak apparently had the capacity to switch partners from *Nothofagus* to species of *Myrtaceae*. Those authors also pointed out that there is another species, *Rozites fusipes* Horak & Taylor (apparently a sister taxon to *R. symeae*), that is associated with *Nothofagus* in New Zealand and with *Nothofagus* and *Eucalyptus* in Tasmania. Bougher (1987) has demonstrated pure culture synthesis of ectomycorrhizas with *Nothofagus* and *Eucalyptus* using isolates of *Descolea maculata* Bougher & Malajczuk from Western Australia eucalypt forests. In the New World, Halling (1989) and later Mueller and Strack (1992) documented similar host shifts of mushroom species from conifers in the United States to oaks in Colombia and Costa Rica.

North/South Clinal Distribution

A general analysis of phenetic similarities in one family and three genera of ectomycorrhizal mushrooms showed greater (at higher taxonomic levels) or lesser (at lower taxonomic levels) affinities with North Temperate taxa of the

Western Hemisphere (Mueller and Halling, 1995). These latter data indicate a definite north/south clinal distribution pattern. For example, species with a distribution range from the North Temperate Zone to southern Colombia would comprise: *Cortinarius iodes* Berk. & M.A. Curtis, *Lactarius indigo* (Schwein.) Fr., *Lactarius atroviridis* Peck (Fig. 1.10), *Laccaria amethystina* Cooke, and *Strobilomyces confusus* Singer. In these particular examples (except for *L. amethystina*), the north temperate distribution is restricted to eastern North America. These taxa exhibit the largest distribution range.

Another clinal pattern describes species with a north temperate to Costa Rica distribution. In this case, one would encounter *Asterophora parasitica* (Fr.) Singer, *Boletus frostii* J.L. Russell (Fig. 1.11), *Lactarius psammicola* A.H. Sm., *Lactarius rimosellus* Peck, *Russula nigricans* (Bull. : Fr.) Fr., and *Tylopilus eximius* (Peck) Singer. While *Asterophora* is an obligate parasite of the obligately ectomycorrhizal *Russula* and widely distributed in the Northern Hemisphere (as is *R. nigricans*), the other species are part of the eastern North American mycota.

Local Endemism

In the montane Neotropics of Central and northern South America, observations show that there are degrees of apparent endemism with species ranging from locally distributed to quite restricted. Some Neotropical oak endemics are *Amanita garabitoana* nom. prov., *Laccaria gomezii* G.M. Mueller & Singer (Fig. 1.12), *Lactarius costaricensis* Singer, *Leccinum andinum* Halling, and *R. colombiana*. Here, it is important to note that the genera are widespread north

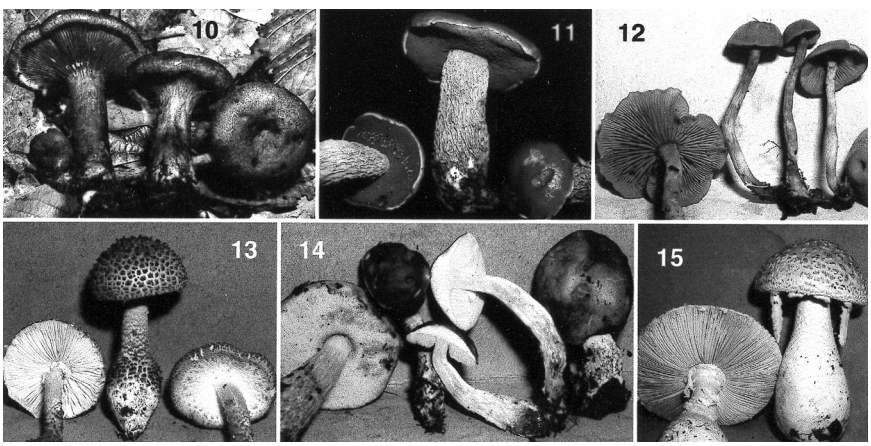

Fig. 1.10. *Lactarius atroviridis* (× 0.39). **Fig. 1.11.** *Boletus frostii* (× 0.19). **Fig. 1.12.** *Laccaria gomezii* (× 0.39). **Fig. 1.13.** *Amanita costaricensis* nom. prov. (× 0.10). **Fig. 1.14.** *Leccinum talamancae* (× 0.19). **Fig. 1.15.** *Amanita conara* nom. prov. (× 0.10).

temperate entities (except see discussion of *Rozites* above), but the species appear endemic to the montane Neotropics. Currently, in the case of more restricted endemics, one would encounter *Amanita costaricensis* nom. prov. (Fig. 1.13), *Leccinum talamancae* Halling, Gómez, & Lannoy (Fig. 1.14), *Amanita conara* nom. prov. (Fig. 1.15), *Boleus flavoniger* Halling, G.M. Mueller, & Gómez, and *Tricholosporum violaceum* Halling & Franco-M. As mentioned above, the genera are widespread north temperate taxa, but the species appear to be locally restricted to only a few sites in the Cordillera Talamanca of Costa Rica.

Generic Similarity

The *Boletaceae* are a conspicuous element in any north temperate woodland ecosystem. Oak forests of the montane Neotropics are no exception. In an analysis of 24 bolete genera *sensu* Singer (1986), which are almost always ectomycorrhizal, 18 occur in Costa Rica and Colombia (Neotropical oak forests) with a relative similarity of ± 94% with the North Temperate Zone (cf. Mueller and Halling, 1995; Halling, 1997b). These data would add support to the aforementioned conclusions that ectomycorrhizal plants (like oaks) migrated from the Northern Hemisphere. In addition, it appears that whole communities migrated (plants and mycorrhizal fungi, as well as obligate parasites of cited fungi).

Species Similarity

Halling (1997b) provided evidence that the overlap of species similarity of selected genera of boletes with the North Temperate Zone was low, ranging from one-fifth to less than one-half. However, not mentioned in that publication is the fact that Neotropical bolete species are most closely allied with species from eastern North America (e.g. *B. flavoniger* is an ally with *Boletus ornatipes* Peck and *Boletus retipes* Berk. & M.A. Curtis (Halling, 1997b)).

Macromycete Diversity

In a survey of 0.1 ha (1000 m^2) in the Cordillera Talamanca, Costa Rica (G.M. Mueller and R.E. Halling, Chicago and New York, unpublished data), there are over 200 species of macrofungi in a parcel of native forest that includes only 20–25 species of vascular plants (M. Kappelle, Costa Rica, 1997, personal communication), and just two species of ectomycorrhizal angiosperms (*Quercus seemannii* Liebm. and *Quercus copeyensis* C.H. Muller). Such numbers lend credence to Hawksworth's (1991) hypothesis concerning the world's diversity of fungi. Additional unpublished data from further collecting in Neotropical habitats bolster Hawksworth's contentions.

Conclusions

In summary, apparent restricted distributions of agarics and boletes will always be discovered based on the work of those who frequent under-collected habitats. Relictual disjunct distributions reflect original widespread occurrence of old genomes before continental breakup with little subsequent phenotypic variation. The taxonomic affinities of non-montane, lowland agarics and boletes range from restricted endemics to those with widespread pantropical occurrence. At this time, little can be said about non-Andean, montane agaric biogeography of the Neotropics; few mycologists have collected in those remote sites in the last millennium. Neotropical montane habitats dominated by oak decidedly harbour agarics and boletes with genera and species whose genealogy is derived from the North Temperate Zone. These taxa exhibit a north to south clinal distribution pattern. While generic similarity is high and species similarity low in Neotropical montane oak forests, the expectation is that these trends will remain even as additional diversity is discovered.

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